Diversity and Mega-Targets of Selection from the Characterization of a Barley Collection

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ABSTRACT

Germplasm exchange is essential for assuring genetic gain in a breeding program. Two aspects of breeding programs are relevant to making them compatible for germplasm exchange: the amount of genetic diversity within programs and the identification of breeding programs with similar breeding objectives and environments of selection (i.e., mega-targets of selection). The objective of this study was to develop a data-driven method to group breeding programs likely to be compatible for germplasm exchange and to use phenotypic characterization data of barley (*Hordeum vulgare* L.) from breeding programs to illustrate this method. In two locations in Uruguay we evaluated 20 traits in 353 genotypes of barley from 23 private and public breeding programs distributed worldwide. We found significant amounts of genetic diversity for all traits, but differences in diversity among programs for only seven traits. We identified programs with high (Western Australia Department of Agriculture; University of Saskatchewan; and Svalöf Weibull Ab, Sweden) and low diversity (winter program of Osijek Agricultural Institute, Croatia; spring program of Osijek Agricultural Institute, Croatia; Saatzucht Josef Breun, Germany; Busch Agricultural Resources; USDA-ARS, Aberdeen, ID; and University of Minnesota). We developed a methodology that groups programs with similar performance and response to the environments. We used the methodology to group the 23 breeding programs of barley into sets that might benefit most from germplasm exchange. The identification of compatible programs for germplasm exchange could be relevant for improving genetic gains in breeding programs.

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Abbreviations: DTA, days between planting date and anthesis; DTH, days between planting and heading; ME, mega-environment(s); MTS, mega-target(s) of selection.

Genetic diversity is essential in a breeding program for two reasons: to insure against unforeseeable changes in the environment (Gepts, 2006) and to maintain genetic progress (Gepts, 2006; Rasmusson, 2001). Maintaining every single allele in a breeding population as insurance in case any may be needed in the future is neither possible nor desirable. Trying to broaden the diversity of a breeding program to account for the unknown will only slow genetic progress because the selection intensity on the traits of interest would be very small. Germplasm banks can maintain genetic diversity that is not immediately needed in the breeding program. When new variation is needed because the environment has changed (e.g., a new disease appears), specific genetic variation can be brought into the breeding program. There are several strategies to maintain genetic gain, including the use of elite by elite crosses known as advanced cycle breeding (Bernardo 2002). The use of elite germplasm leads to significant genetic gains in quantitative traits due to the accumulation of favorable alleles (Rasmusson and Phillips, 1997). A desirable genotype for germplasm exchange would therefore be an elite line with new alleles at the loci of interest. For this purpose, assessment of diversity and performance of elite germplasm is needed.

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Germplasm exchange of elite genotypes among breeding programs is an effective way to increase genetic gain. However, not all the elite genotypes will perform well in all the environments. Genotypes are adapted to the environment in which they were selected, and perform best under those conditions (Simmonds, 1991). Furthermore, breeding objectives and the environmental conditions of genotype evaluation shape those adaptations (Atlin et al., 2001; Ceccarelli, 1994). We call the combination of those factors targets of selection. However, it is not easy to identify a priori targets of selection because of the multiple objectives and several environmental conditions of genotype evaluation. Therefore, breeders need data-driven methods to identify compatible programs for germplasm exchange. Broadly speaking, programs will be compatible if they have the same targets of selection (i.e., if they belong to the same mega-target of selection [MTS]). Two aspects of genotype evaluation are relevant in the identification of MTS: genotypic performance and the response of a genotype to a change in the environment. If genotypes are evaluated in the target environment, genotypic performance is an effective way of choosing compatible germplasm. However, it is not possible for a breeding program to evaluate every single genotype. Therefore, comparisons of genotypic performance outside the targeted environment should be considered. In the nontarget environment, grouping genotypes by performance alone is not enough to identify compatible breeding programs. Genotypes could perform poorly for different reasons. For example, one set of genotypes could be limited because of disease pressure, while the other could be limited by photoperiod conditions. Germplasm exchange among those breeding programs would probably not provide an advantage. Therefore, a second key aspect in the identification of targets of selections is the response of a genotype to change in the environment. For example genotypes that produce similar yields under dry and humid conditions would be assigned to a group, while genotypes that perform well in humid conditions but poorly in dry conditions would be assigned to a different group.

Mega-targets of selection are analogous to mega-environments (ME). Mega-environments were first defined as environments with similar "biotic and abiotic stresses, cropping system requirements, consumer preferences, and volume of production" (Braun et al., 1996:177). The concept was later redefined as environments that caused genotypes to perform similarly (Gauch and Zobel, 1996, 1997), and therefore little genotype by environment interaction is expected within ME (Yan et al., 2000). Furthermore, ME were defined in a multi-environment trial context as groups of environments that produce the same rank of genotypes, and where evaluation of genotypes in more than one environment of an ME would produce redundant information (Yan et al., 2000). Following the same principles, in MTS, groups of breeding programs are formed such that germplasm exchanged within a group will be well adapted and respond similarly to the new environmental conditions. To belong to a MTS, breeding programs would have similar mean performance (i.e., the same "volume of production" by the definition of Braun et al., 1996), and respond similarly to new environments (i.e., "no genotype by environment interaction" in Gauch and Zobel's [1996] definition).

Barley (*Hordeum vulgare* L.) is a good model species for the combined study of diversity and targets of selection. It was one of the first crops to be domesticated 10,000 yr ago (Harlan, 1971) and has undergone intensive breeding for more than one century (van Hintum, 1994). Despite the long history of breeding, barley is still a highly diverse crop and is adapted to a range of environmental conditions (Hayes et al., 2003), including tolerance to cold, drought, alkalinity, and salinity. Furthermore, breeding efforts have produced systematic genetic gain in barley for several traits (Gymer, 1981) despite the common use of elite parents that created narrow gene pools (Rasmusson and Phillips, 1997). Therefore, different targets of selection are expected, and breeders would benefit from the identification of breeding programs between which germplasm exchange would be advantageous.

The aim of this study was to develop a data-driven method to group breeding programs likely to be compatible for germplasm exchange and to use phenotypic characterization data of barley from breeding programs to illustrate this method. Our four specific objectives were (i) to characterize genetic diversity of traits in advanced lines of barley from selected breeding programs; (ii) to describe the diversity of the breeding programs for those traits; (iii) to develop a data-driven method identifying MTS in barley to group programs likely to be compatible for germplasm exchange; and (iv) to use the barley characterization data to illustrate the use of MTS.

MATERIALS AND METHODS

Materials

A total of 353 inbred lines of barley from 23 private and public breeding programs was evaluated. Each breeder responsible for a breeding program was asked to provide 20 advanced lines or recently released cultivars that represented current diversity in their program. Two-row and six-row types were treated separately; if a breeding program included both, separate samples were asked of each type. The programs that provided seed were from the United States (Washington State University [Washington]; University of Minnesota [Minnesota]; two-row and six-row programs of North Dakota State University [North Dakota]; two-row and six-row programs of USDA-ARS Aberdeen, ID [Idaho]; two-row, six-row, and international programs of Busch Agricultural Resources [Busch Ag Res]), Canada (University of Saskatchewan [Canada Saskatchewan]; Alberta Agriculture, Food and Rural Development [Canada Alberta]), Europe (Saatzucht Josef Breun in Germany

[Germany]; Svalöf Weibull Ab in Sweden [Sweden]; the Abed Foundation in Denmark [Denmark]; the spring and winter programs from Osijek Agricultural Institute of Croatia [Croatia spring and Croatia winter, respectively), Australia (University of Adelaide [Adelaide]; Western Australia Department of Agriculture [Western Australia]), and South America (National Agronomic Research Institutes of Chile and Uruguay [Chile and Uruguay, respectively]).

Five checks were also included to complete the experimental design (i.e., to have a square row-column design of 20 by 20 plots) and to serve as controls for heading dates. Checks were 'Dayman', 'Perun', 'Ceibo', 'Clipper', and 'Quebracho'. Data on checks are not reported.

Field Trials

All genotypes were evaluated in a row–column (alpha lattice) design with 20 rows, 20 columns, and 3 replications. Twenty seeds from each genotype were sown in a hill-plot. Each hill-plot column had a spacing of 0.4 m on one side and 0.6 m on the other side. Within-row spacing was 0.4 m. Evaluations were conducted in 2005 at two locations in Uruguay. Colonia is in southwest Uruguay (34°20′24″ S, 57°42′36″ W, and 81 m altitude) and has fine, smectitic, thermic, Vertic Argiudol soils, while Young is in northern Uruguay (32°40′48″ S, 57°40′12″ W, and 80 m altitude) and has fine, smectitic, thermic, Typic Hapludert soils.

Although Colonia and Young are distinct environments (described below), they do not represent all the possible growing environments of barley worldwide. We used these environments to present the methodology of MTS and not to propose strong global recommendations of germplasm exchange. To accomplish the more ambitious objective of global recommendations of germplasm exchange, the characterization of the genotypes should be conducted in even more contrasting environments than Young and Colonia. However, the use of more contrasting environments would not improve presentation of the methodology.

Colonia has a milder climate than Young with the following characteristics for Colonia and Young, respectively: mean annual temperature of 16.5 and 17.9°C, average maximum temperature of 21.8 and 23.8°C, average temperature of the hottest month of 29.4 and 31.5°C, average minimum temperature of 11.7 and 12.2°C, average temperature of the coldest month of 6.9 and 6.5°C, average relative humidity of 74.4 and 73.0%, and annual precipitation of 1073 and 1218 mm. Additionally, soils in Colonia are rich in organic matter, while soils in Young are more sandy. The differences among the two environments are important. However, for illustration purposes we compare the climate of Colonia and Young to that found in one of the breeding programs included in the study, Adelaide, Australia. The temperature in Adelaide is very similar to that in Colonia (average maximum and minimum temperatures are 21.8 and 12.1°C, respectively, and average temperature of the hottest and coldest month are 29.0 and 7.7°C, respectively). Therefore, differences in temperature among Colonia and Young are larger than differences among Colonia and Adelaide. However, the difference in precipitation and relative humidity between Adelaide and either Uruguayan environment is stronger than among Uruguayan environments (i.e., 518 mm of precipitation and 49.5% of relative humidity in Adelaide).

Seeding date was typical for the region, occurring on 21 July and 30 July for Colonia and Young, respectively. Seed emergence was 30 July and 6 August. Plots were fertilized with 45 kg ha^{-1} of urea to reach 40 mg kg^{-1} of nitrogen as NO_3^- at planting and nitrogen in plant was measured to adjust doses at the end of tillering but no nitrogen addition was needed. Given the disparity of origins of the materials, diseases were an important threat to plant survival. Therefore, weekly monitoring for disease was performed and a systemic fungicide was applied when such a threat appeared and after disease scoring was completed. Each application consisted of 1 L ha^{-1} of the commercial fungicide Opera (BASF Uruguaya S.A., Montevideo, Uruguay; 133 g ha^{-1} of pyraclostrobin (methyl [2–[[[1–(4–chlorophenyl)–1*H*–pyrazol–3–yl] oxy]methyl]phenyl] methoxycarbamate) and 50 g ha^{-1} of epoxiconazole ((2*RS*,3*RS*)–1–[3–(2–chlorophenyl)–2,3–epoxy–2–(4–fluorophenyl)propyl]–1*H*–1,2,4–triazole). We applied fungicide twice in Colonia (7 September and 15 October), and once in Young (22 September). Full-plots were harvested on 7 December and 5 December for Colonia and Young, respectively.

Several traits were recorded for each line either on plots or on individual plants. Traits measured on a plot level were total number of tillers (all tillers present at the end of tillering in a hill-plot of 0.2 m^2 area were counted); spot blotch disease caused by *Bipolaris sorokiniana* (Sacc.) Shoem. [teleomorph: *Cochliobolus sativus* (Ito and Kurib.)] (scoring from 1 to 5, where 1 is low and 5 is high); leaf rust disease caused by *Puccinia hordei* G. Otth. (scoring from 1 to 5, where 1 is low and 5 is high); powdery mildew disease caused by *Blumeria* (=*Erysiphe*) *graminis* (DC.) E.O. Speer f. sp. *hordei* Ém. Marchal (scoring from 1 to 5, where 1 is low and 5 is high); total number of days between planting date and anthesis (DTA; recorded when 50% of the plants flowered); total number of days between planting and heading (DTH; recorded when 50% of the plants headed); plant height (measured from the ground to the tips of most spikes, cm); biomass at plant maturity (g m^{-2}); grain yield (g m^{-2}); total number of spikes (all spikes present at maturity in a hill plot of 0.2 m^2 area were counted); test weight (measured on a volume of 6 mL, g L^{-1}); and weight of 100 kernels (g).

Five plants from each plot were chosen at random at flowering time and were color-marked with plastic twist-bands. Measurement of traits on single plants instead of whole plots decreased experimental error and allowed estimation of within-plot variation. The following traits were measured on each individual plant: flag leaf length (measured from the ligulae to the tip of the leaf, cm), flag leaf width (measured at 2.5 cm from the ligulae, cm), spike length (measured from the base to the tip of the spike, without counting the awns, cm), awn length (measured from the top of the spike to the tip of the longest awn, cm), peduncle length (measured from the last node to the base of the spike, cm), flag leaf height (measured from the ground to the ligulae of the flag leaf, cm), spike height (measured from the ground to the base of the spike, in cm), and number of grains per spike.

Statistical Models

Traits measured at the plot and plant levels were modeled according to the following linear models, respectively:

$$Y_{ijklmn} = B_{ij} + R_{k(ij)} + C_{l(ij)} + P_m + G_{n(m)} + \varepsilon_{ijklmn} \quad [1]$$

$$Y_{ijklmnop} = B_{ij} + R_{k(ij)} + C_{l(ij)} + P_m + G_{n(m)} + I_{o(ijk)} + \varepsilon_{ijklmnop} \quad [2]$$

where B_{ij} = effect of jth block in environment i, $R_{k(ij)}$ = effect of kth row in the ijth block–environment, $C_{l(ij)}$ = effect of lth column in the ijth block–environment, P_m = effect of mth breeding program, $G_{n(m)}$ = effect of nth genotype in the mth breeding program, $I_{o(ijk)}$ = effect of the oth plot in the ijth block–environment, e_{ijklmn} = residual error for the nth genotype in the mth breeding program in the ijth block-environment, and $e_{ijklmnop}$ = residual error for the pth plant of the nth genotype of the mth breeding program in the ijth block–environment. Plants within a plot share similarities from belonging to the same plot, therefore, the plot effect ($I_{o(ijk)}$) was included in the linear model for plant-level variables (Eq. [2]).

We defined a hierarchical Bayesian model following Edwards and Jannink (2006), which allowed for heterogeneous genotypic variance within populations. We modeled both means (B_{ij}, $R_{k(ij)}$, $C_{l(ij)}$, P_m, $G_{n(m)}$, and $I_{o(ijk)}$) and associated variances (σ^2_R, σ^2_C, σ^2_P, $\sigma^2_{G(m)}$, σ^2_I, and σ^2). At the first level of the Bayesian hierarchy, observations were modeled as independent samples from a normal distribution:

$$Y_{ijklmn} \mid B_{ij}, R_{k(ij)}, C_{l(ij)}, P_m, G_{n(m)}, \sigma^2 \sim N\left(B_{ij} + R_{k(ij)} + C_{l(ij)} + P_m + G_{n(m)}, \sigma^2\right)$$

$$Y_{ijklmnop} \mid B_{ij}, R_{k(ij)}, C_{l(ij)}, P_m, G_{n(m)}, I_{o(ijk)} \sim N\left(B_{ij} + R_{k(ij)} + C_{l(ij)} + P_m + G_{n(m)} + I_{o(ijk)}, \sigma^2\right).$$

The second level of the Bayesian hierarchy includes prior distributions for means B_{ij}, $R_{k(ij)}$, $C_{l(ij)}$, P_m, $G_{n(m)}$, and $I_{o(ijk)}$, and error variance σ^2. Priors on all location parameters were normal with mean zero and variances defined to condition the desired level of information sharing among levels of the factor. For block-environment means, B_{ij}, the prior was defined with a very large variance to make the prior noninformative: $B_{ij} \sim N(0, 10^{-7})$. The flat and independent prior is a Bayesian equivalent to defining the block effect as a fixed effect in classical linear models. We did not include location effects in our model so that all parameters were estimable.

Row, column, breeding program, genotype, and plot were modeled with priors that treated them akin to random effects in classical mixed linear models. Row, column, population, and plot effects were modeled as samples from a normal distribution with variance σ^2_R, σ^2_C, σ^2_P, and σ^2_I, respectively: $R_{k(ij)} \mid \sigma^2_R \sim N(0, \sigma^2_R)$, $C_{l(ij)} \mid \sigma^2_C \sim N(0, \sigma^2_C)$, $P_m \mid \sigma^2_P \sim N(0, \sigma^2_P)$, $I_{o(ijk)} \mid \sigma^2_I \sim N(0, \sigma^2_I)$.

Genotype effects were modeled as samples from a normal distribution with variance of the genotype effect as a function of the breeding program: $G_{n(m)} \mid \sigma^2_{G(m)} \sim N(0, \sigma^2_{G(m)})$. The subscripted notation on the variance of genotype indicates that every breeding program had a unique genotypic variance. Variance of the genotype, $\sigma^2_{G(m)}$, was modeled with a generalized linear model using a natural-log link function: $\ln(\sigma^2_{G(m)}) = a + ap_m$. Where a is the average natural logarithm of the genotypic variance, and ap_m is the breeding program effect on the natural logarithm of the genotypic variance. The parameter a conditions an average variance across all genotypes. The parameter ap_m describes the degree to which the genotypic variance tends to be higher for observations on some breeding programs (positive values of ap_m), and lower for observations on other breeding programs (negative ap_m values). The parameters a and ap_m were specified as $a \sim N(0, 10^7)$, and $ap_m \mid \sigma^2_{GP} \sim N(0, \sigma^2_{GP})$. σ^2_{GP} express the degree of heterogeneity of genotypic variance within breeding programs. Homogenous within-breeding-program genotypic variances would correspond to $\sigma^2_{GP} = 0$, while large σ^2_{GP} would indicate heterogeneous within-breeding-program genotypic variances. Therefore, a test of $\sigma^2_{GP} = 0$ is a test of homogeneity of genetic variance within breeding programs.

σ^2_{GP} was given noninformative priors: $\sigma^2_{GP} \sim IG(0.0001, 0.0001)$. Priors on the variance of row, column, and breeding program effects were chosen to be noninformative as $\sigma^2_R \sim IG(0.0001, 0.0001)$, $\sigma^2_C \sim IG(0.0001, 0.0001)$, $\sigma^2_P \sim IG(0.0001, 0.0001)$. Residual variance was also modeled as $\sigma^2 \sim IG(0.0001, 0.0001)$. All parameters were estimated via Markov Chain Monte Carlo simulation using the Bayesian Gibbs Sampling software WINBUGS (Spiegelhalter et al., 2003).

Statistical Analysis

All analyses were performed accounting for head type (i.e., two-row or six-row barleys) because they represent the two most distinct germplasm pools in barley (Powell et al., 1990; Takahashi et al., 1975). Depending on the specific analysis, we either included head type in the linear model, or we performed the analysis for two- and six-row populations separately.

Least-squares means of breeding programs for all traits were obtained using the linear models described above for plot (Eq. [1]) and plant (Eq. [2]) variables, but including head type in the model. Means were subject to principal component and cluster analysis using SAS statistical software (SAS Institute, 2004). We used the Ward method (Ward, 1963) of clustering to group breeding programs with similar performance (i.e., similar means) for all variables. It is a hierarchical method that groups breeding programs producing the least increase in the sum of squares within groups (Manly, 1988). Consequently, breeding programs with similar means for all the variables should be assigned to the same clusters. The cubic clustering criterion and pseudo-F were used to decide on the number of groups (SAS Institute, 2004; Franco et al., 2005).

Least-squares means of genotypes for all traits were obtained using the linear models described above for plot (Eq. [1]) and plant level (Eq. [2]) variables, with head type in the model and genotypes as fixed effects. A stepwise discriminant analysis on genotypic means in SAS (SAS Institute, 2004) was used to identify the traits that best discriminated among two-row and six-row types, and among breeding programs. A STEPWISE selection method and a 15% significance level ($P \leq 0.15$) were used (Gutierrez et al., 2003; Franco et al., 1998). Neither leaf rust disease nor peduncle length were included in the discriminant analysis. Leaf rust disease was fitted using only one location (Colonia) because there was not a significant outbreak of the disease in the other location. Peduncle length, in contrast, had a high number of missing values for some genotypes. Genotypic means were also used to identify the best performing genotypes for each variable in two- and six-row types.

We tested whether there were significant differences in the amount of genetic variance within breeding programs (σ^2_{GP}) in WINBUGS (Spiegelhalter et al., 2003) by using the highest posterior density intervals (Gelman et al., 2003) of σ^2_{GP}. Once a variable was identified as having a significant difference in the amount of genetic variance within breeding programs ($\sigma^2_{GP} > 0$), nonoverlapping 95% credible intervals were used to identify the least and most diverse breeding programs.

We also grouped breeding programs by their response to a change in the environment. For this purpose, least-squares means of breeding programs by location were obtained. The difference in mean values between the two locations was subject to cluster analysis using the Ward method (Ward, 1963) in SAS (SAS Institute, 2004). This procedure grouped breeding programs that had similar responses across variables to the change in the environment, and therefore would produce the least increase in the sum of squares within groups. If we assume only one variable, for example, grain yield, two breeding programs that had high yields in one environment and low yields in the second (i.e., they had high values for the response variable: yield in location 1 − yield in location 2) would be assigned to the same cluster. On the other hand, breeding programs with minimal difference in yield among locations (response variable close to zero) would be assigned to a different cluster. Again, neither leaf rust disease nor peduncle length were used for this analysis. Additionally, the Germany breeding program was excluded from this analysis because there was not enough seed to plant the genotypes in both locations. The cubic clustering criterion and pseudo-F were used to decide on the number of groups (SAS Institute, 2004; Franco et al., 2005).

RESULTS AND DISCUSSION

Mean Performance of Breeding Programs

There were significant differences ($P < 0.0001$) among breeding programs for all the variables analyzed (data not shown). We present results for two- and six-row barley in turn. The programs with highest least-squared means for grain yield in our test locations were Croatia spring, Uruguay, and North Dakota, while the lowest yields were from Chile and Croatia winter programs (Table 1). We expected Uruguay to be among the highest yielding breeding programs because of the adaptation to the environment, and breeding efforts conducted in those environments (Díaz and Germán, 2005). The Uruguayan program had the highest test weight, while North Dakota, Uruguay, and Australia had the highest weight of 100 grains. Alberta Canada was the program with the highest number of grains (Table 2). North Dakotan, Australian, and Uruguayan programs were the earliest maturing programs (DTA and DTH, Table 1). Early maturity is a desirable trait in the northern Great Plains (e.g., North Dakota) because of producers' preferences (Urrea et al., 2005); therefore early maturing genotypes were selected for in North Dakota. Despite long growing seasons described for both Australia and Uruguay, with late maturing genotypes produced for Australia (Jettner et al., 2003), and early to late maturing genotypes for Uruguay (Díaz and Germán, 2005); both programs were among the earliest maturing programs. Large photoperiodic responses of their genotypes, which caused them to shorten their cycle in later sowing seasons, were reported for the Uruguayan genotypes (Díaz and Germán, 2005). Additionally, they were among the most diverse programs for maturity (see results below). Our experiment was conducted during typical to late growing seasons; therefore, the photoperiodic response was probably the cause of the early maturing behavior of the genotypes described above. European, Australian, and the international program of Busch Ag Res had the shortest plants on average, and Canada and North Dakota had the tallest plants (plant height). The high incidence of the semi-dwarfing gene *sdw1* in European germplasm was responsible for the short plants of European genotypes (Ramsay et al., 2004). European programs had low incidence of powdery mildew (Table 1). Lower incidence of powdery mildew in European lines was expected because the disease is common in Europe and there is a long history of breeding for resistance (Jensen et al., 1992; Friedt et al., 2000), while powdery mildew is not an important disease in North America and therefore little attention is given to resistance to this disease (Molina-Cano et al., 2003).

In the case of six-row barley, the highest least-squared means for grain yields and test weight were from the Minnesota and Idaho breeding programs, while the lowest were from Croatia winter (Table 1). The smallest number of grains per spike was obtained for Croatia winter, while the other programs had similar number of grains (Table 2). The earliest maturing (DTA and DTH) program was Minnesota, and the winter program of Croatia had the lowest incidence of powdery mildew and leaf rust (Table 1). Again, selection for early maturity in the northern Great Plains (Urrea et al., 2005) explains the results found for Minnesota. Low incidence of powdery mildew is selected for in European genotypes (Jensen et al., 1992; Friedt et al., 2000), explaining Croatia behavior.

Mean Performance of Individual Genotypes

In the previous section we compared means of breeding programs, while here we compare performance of single genotypes (a genotype might be among the highest yielders even if the breeding program to which it belongs did not have high mean yield). The variance among genotypes within breeding programs was significantly different from zero ($P < 0.05$) for all variables except spot blotch disease (data not shown). The two-row genotypes that produced the highest grain yields in our study were from Uruguay and the spring program of Croatia (Table 3). While the six-row genotypes that yielded the most were from Canada Alberta and Busch Ag Res breeding programs. The earliest maturing two-row and six-row genotypes were from the Australia and Minnesota breeding programs,

Table 1. Mean breeding program values and standard errors (in parenthesis) and least and most diverse programs for the traits measured at the plot level: number of tillers (NTIL), spot blotch disease (SB), leaf rust disease (LR), powdery mildew disease (PM), days until anthesis (DTA), days until heading (DTH), plant height (HTOT), biomass (BWT), grain yield (YLD), number of spikes (NSPK), test weight (TWT), and weight of 100 grains (W100G).

BP†	N	NTIL		SB		LR		PM		DTA		DTH		HTOT		BWT		YLD		NSPK		TWT		W100G	
				0 = low, 5 = high						d				cm		g m^{-2}						g L^{-1}		g	
Two-row																									
AU-AD	20	78.4	(4.3)	1.6	(0.1)	2.3	(0.1)	1.7	(0.2)	80.8	(1.3)‡	89.8	(1.4)	70.4	(1.7)	657.5	(5.4)	250.7	(12.1)	79.2	(4.7)	686.6	(8.5)‡	5.0	(0.1)‡
AU-WE	15	69.3	(4.6)	1.7	(0.1)	2.7	(0.2)	2.1	(0.2)	82.8	(1.5)§	90.4	(1.5)§	72.2	(1.7)	604.0	(5.8)	218.8	(13.1)	71.6	(5.1)	680.4	(8.7)‡	5.0	(0.1)§
CA-AB	7	78.6	(5.5)	1.7	(0.1)	2.6	(0.2)	1.9	(0.2)	90.1	(1.5)‡	96.8	(1.6)‡	81.0	(2.0)	712.5	(7.0)	221.8	(15.7)	79.4	(5.5)	659.9	(11.6)‡	4.2	(0.1)‡
CA-SK	16	76.2	(4.6)	1.5	(0.1)	2.8	(0.2)	2.4	(0.2)	88.5	(1.2)‡	96.0	(1.2)	82.4	(1.8)	764.0	(5.8)	246.6	(13.0)	80.4	(5.0)	690.7	(11.6)§	4.5	(0.1)§
CL	4	60.7	(6.9)	1.6	(0.2)	2.9	(0.2)	1.7	(0.3)	92.1	(1.7)‡	100.7	(1.8)‡	77.6	(2.6)	534.5	(9.3)	180.9	(21.0)	58.5	(6.5)	675.3	(17.6)‡	4.5	(0.2)‡
CRO-SP	20	82.1	(4.3)	2.0	(0.1)	2.3	(0.1)	1.3	(0.2)	86.8	(1.2)‡	95.4	(1.2)‡	76.1	(1.6)	770.0	(5.5)	287.9	(12.5)	83.6	(4.8)	701.3	(8.7)‡	4.6	(0.1)‡
CRO-WI	15	94.9	(4.7)	1.4	(0.1)	2.8	(0.2)	2.0	(0.2)	95.0	(1.3)‡	101.1	(1.4)	77.4	(1.7)	580.5	(5.9)	182.5	(13.3)	59.3	(4.9)	653.3	(9.3)‡	4.7	(0.1)‡
DE	20	91.5	(4.5)	2.0	(0.1)	2.9	(0.1)	0.8	(0.2)	91.1	(1.3)‡	98.8	(1.2)‡	70.2	(1.6)	727.0	(5.4)	258.4	(12.3)	89.3	(4.8)	659.2	(9.7)§	4.6	(0.1)§
GE	20	77.1	(5.8)	1.5	(0.2)	2.3	(0.2)	1.8	(0.2)	91.7	(1.5)‡	99.1	(1.6)‡	76.3	(2.0)	651.0	(8.5)	206.7	(18.4)	77.9	(6.2)	677.2	(12.0)‡	4.8	(0.1)‡
SW	20	82.2	(4.4)	2.0	(0.1)	2.5	(0.1)	1.3	(0.2)	91.7	(1.2)‡	97.7	(1.3)	73.3	(1.6)	647.5	(5.5)	213.6	(12.1)	78.8	(4.8)	670.6	(9.2)§	4.5	(0.1)‡
US-BS	18	80.0	(4.3)	1.6	(0.1)	3.0	(0.1)	2.4	(0.2)	89.0	(1.2)‡	96.7	(1.2)‡	79.3	(1.6)	765.5	(5.6)	237.7	(12.5)	84.6	(4.9)	638.7	(8.3)‡	4.3	(0.1)‡
US-BSI	17	78.1	(4.5)	1.9	(0.1)	2.8	(0.1)	1.1	(0.2)	89.5	(1.4)	95.8	(1.4)	73.8	(1.6)	686.0	(5.7)	247.0	(12.7)	78.0	(4.8)	695.4	(8.9)‡	4.7	(0.1)‡
US-ID	13	76.5	(5.0)	1.6	(0.1)	3.3	(0.2)	2.4	(0.2)	88.4	(1.3)‡	95.5	(1.3)‡	78.5	(1.7)	677.5	(6.0)	222.9	(13.4)	77.5	(5.1)	648.8	(9.2)‡	4.4	(0.1)‡
US-ND	20	66.2	(4.3)	1.7	(0.1)	3.0	(0.1)	2.9	(0.2)	80.6	(1.3)‡	88.4	(1.4)	85.6	(1.6)	756.0	(5.4)	261.3	(12.3)	75.2	(4.7)	695.0	(8.3)‡	5.3	(0.1)‡
US-WS	19	82.1	(4.4)	1.8	(0.1)	2.9	(0.1)	2.1	(0.2)	88.5	(1.2)‡	96.1	(1.3)‡	76.6	(1.6)	732.5	(5.4)	256.5	(12.2)	83.8	(5.3)	666.6	(8.7)‡	4.6	(0.1)‡
UY	19	76.7	(4.3)	1.7	(0.1)	2.6	(0.1)	1.5	(0.2)	83.5	(1.3)‡	91.0	(1.3)	77.2	(1.7)	716.0	(5.5)	270.7	(12.4)	78.8	(4.8)	708.7	(9.0)‡	5.1	(0.1)‡
Six-row																									
CA-AB	14	57.9	(4.8)	1.3	(0.1)	3.3	(0.2)	2.4	(0.2)	84.8	(1.4)‡	90.5	(1.5)‡	77.7	(1.8)	635.5	(6.1)	219.0	(13.7)	48.3	(5.0)	649.8	(11.4)§	3.9	(0.1)‡
CA-SK	5	49.5	(6.2)	1.3	(0.2)	3.2	(0.2)	2.1	(0.3)	87.5	(1.9)‡	93.2	(1.7)	80.9	(2.9)	546.5	(8.2)	196.2	(18.0)	37.9	(6.0)	646.3	(13.1)‡	4.1	(0.2)‡
CRO-WI	4	91.7	(6.7)	1.3	(0.2)	3.0	(0.2)	1.9	(0.3)	93.4	(1.8)‡	100.9	(1.8)‡	77.0	(2.4)	558.0	(9.2)	168.4	(21.5)	49.1	(6.5)	645.3	(15.4)‡	4.1	(0.2)‡
US-BS	18	45.2	(4.4)	1.3	(0.1)	3.4	(0.1)	2.8	(0.2)	83.2	(1.2)‡	89.8	(1.3)	86.0	(1.6)	614.5	(5.6)	230.9	(12.5)	37.9	(4.8)	669.1	(8.3)‡	4.4	(0.1)‡
US-ID	7	48.5	(5.6)	1.3	(0.1)	3.4	(0.2)	2.4	(0.2)	82.1	(1.5)‡	88.4	(1.6)‡	84.4	(1.9)	616.0	(7.3)	233.3	(16.3)	39.6	(5.5)	648.2	(12.0)‡	4.4	(0.1)‡
US-MN	20	43.7	(4.3)	1.4	(0.1)	3.8	(0.1)	2.8	(0.2)	80.8	(1.2)‡	87.2	(1.2)‡	82.8	(1.6)	608.0	(5.4)	233.2	(12.1)	38.2	(4.7)	669.5	(8.1)‡	4.6	(0.1)‡
US-ND	15	54.5	(4.5)	1.2	(0.1)	3.2	(0.2)	2.8	(0.2)	82.9	(1.2)‡	88.6	(1.2)‡	90.2	(1.8)	625.0	(5.8)	211.7	(12.9)	43.6	(4.8)	650.7	(9.8)§	4.2	(0.1)‡
GVW¶		0.314	(0.46)	0.247	(0.45)	0.167	(0.30)	0.508	(0.45)	0.247	(0.45)*	0.167	(0.30)*	0.508	(0.45)	0.801	(0.49)	0.167	(0.30)	0.508	(0.45)	0.801	(0.49)*	1.166	(0.77)*

*Significant at the 0.05 level.

†BP, breeding programs; AU-AD, University of Adelaide, Australia; AU-WE, Western Australia Department of Agriculture, Australia; CA-AB, Alberta Agriculture, Food and Rural Development, Canada; CA-SK, University of Saskatchewan, Canada; CL, National Agricultural and Livestock Research Institute, Chile; CRO-SP, spring program of Osijek Agricultural Institute, Croatia; CRO-WI, winter program of Osijek Agricultural Institute, Croatia; DE, the Abed Foundation, Denmark; GE, Saatzucht Josef Breun, Germany; SW, Svalöf Weibull Ab, Sweden; US-BS, Busch Agricultural Resources, USA; US-BSI, international program of Busch Agricultural Resources; US-ID, USDA-ARS, Aberdeen, ID, USA; US-MN, University of Minnesota, USA; US-ND, North Dakota State University, USA; US-WS, Washington State University, USA; UY, National Agricultural and Livestock Research Institute, Uruguay.

‡Least diverse programs for the traits measured at the plot level.

§Most diverse programs for the traits measured at the plot level.

¶GVW, variance in the genetic variance within breeding programs.

Table 2. Mean breeding program values and standard errors (in parenthesis) and least and most diverse programs for the traits measured at the plant level: flag leaf length (FLL), flag leaf width (FLW), spike length (SLT), awn length (ALT), flag leaf height (FLH), spike height (SHT), peduncle length (PEDL), and number of grains per spike (NG).

BP†	FLL		FLW		SLT		ALT		FLH		SHT		PEDL		NG	
	cm															
Two-row																
AU-AD	11.4	(0.6)	0.75	(0.1)	8.2	(0.2)	12.1	(0.3)	65.6	(1.2)	66.6	(1.8)‡	5.6	(1.0)	24.5	(3.2)‡
AU-WE	12.2	(0.7)	0.75	(0.1)	9.0	(0.2)	10.9	(0.2)‡	67.9	(1.2)	69.6	(1.8)‡	5.1	(1.0)	25.4	(3.2)‡
CA-AB	14.8	(0.8)	0.97	(0.1)	10.0	(0.3)	10.5	(0.3)‡	72.6	(1.5)	76.8	(2.0)‡	6.1	(1.2)	33.1	(3.6)§
CA-SK	13.4	(0.6)	0.84	(0.1)	9.7	(0.2)	11.3	(0.3)§	72.1	(1.3)	75.3	(2.1)§	6.3	(1.0)	28.8	(3.2)‡
CL	14.1	(1.0)	0.81	(0.1)	9.6	(0.3)	12.1	(0.4)‡	70.4	(1.8)	72.1	(2.5)	5.9	(1.5)	28.7	(3.9)‡
CRO-SP	12.5	(0.7)	0.72	(0.1)	8.7	(0.2)	11.3	(0.2)‡	71.2	(1.1)	72.9	(1.6)‡	4.5	(1.0)	27.1	(3.3)‡
CRO-WI	11.3	(0.7)	0.69	(0.1)	9.4	(0.2)	10.8	(0.3)‡	70.6	(1.3)	72.2	(1.7)‡	1.8	(1.1)	27.3	(3.2)‡
DE	11.7	(0.6)	0.66	(0.1)	9.1	(0.2)	11.7	(0.3)	67.9	(1.1)	65.0	(1.5)‡	0.6	(0.9)	26.7	(3.2)‡
GE	12.2	(0.7)	0.72	(0.1)	9.6	(0.2)	11.7	(0.3)‡	71.9	(1.3)	71.6	(1.7)‡	5.6	(3.2)	27.3	(3.4)‡
SW	13.3	(0.7)	0.77	(0.1)	9.4	(0.2)	11.0	(0.3)§	69.8	(1.1)	69.0	(1.6)‡	3.6	(1.0)	27.9	(3.3)§
US-BS	12.5	(0.7)	0.88	(0.1)	9.4	(0.2)	11.3	(0.2)‡	71.6	(1.1)	75.1	(1.5)‡	5.7	(1.0)	29.2	(3.4)‡
US-BSI	12.2	(0.7)	0.72	(0.1)	9.2	(0.2)	11.6	(0.2)‡	69.7	(1.2)	69.1	(1.5)‡	2.2	(1.0)	26.4	(3.2)‡
US-ID	13.1	(0.7)	0.79	(0.1)	9.4	(0.2)	11.3	(0.3)	72.5	(1.3)	75.7	(1.8)‡	5.8	(1.1)	28.3	(3.2)‡
US-ND	15.0	(0.7)	1.02	(0.1)	9.2	(0.2)	10.8	(0.2)‡	73.3	(1.1)	79.8	(1.5)‡	9.8	(0.9)	26.8	(3.3)
US-WS	12.4	(0.7)	0.73	(0.1)	9.1	(0.2)	11.6	(0.3)	71.7	(1.1)	72.9	(1.6)‡	3.9	(0.9)	29.2	(3.4)§
UY	12.5	(0.7)	0.76	(0.1)	8.6	(0.2)	11.5	(0.2)‡	71.2	(1.2)	73.6	(1.7)‡	6.6	(1.0)	25.7	(3.2)‡
Six-row																
CA-AB	17.3	(0.7)	1.63	(0.1)	9.1	(0.2)	10.3	(0.3)§	67.6	(1.4)	72.3	(2.0)§	7.6	(1.1)	63.5	(3.3)‡
CA-SK	15.4	(0.9)	1.48	(0.1)	8.8	(0.3)	10.4	(0.4)‡	71.9	(1.9)	76.0	(3.0)§	5.9	(1.4)	59.4	(4.3)‡
CRO-WI	10.6	(1.0)	0.72	(0.1)	8.2	(0.3)	11.6	(0.4)‡	71.5	(1.8)	72.0	(2.4)‡	0.8	(1.6)	52.0	(4.4)‡
US-BS	17.9	(0.7)	1.67	(0.1)	8.8	(0.2)	10.7	(0.2)‡	73.1	(1.2)	80.3	(1.5)‡	8.6	(1.0)	62.4	(3.3)‡
US-ID	16.6	(0.9)	1.52	(0.1)	8.7	(0.3)	10.5	(0.3)‡	71.3	(1.5)	78.4	(1.9)‡	10.2	(1.2)	63.4	(3.3)‡
US-MN	18.7	(0.7)	1.67	(0.1)	8.8	(0.2)	10.7	(0.2)‡	70.6	(1.1)	77.4	(1.6)‡	9.9	(1.0)	61.2	(3.3)‡
US-ND	17.1	(0.7)	1.66	(0.1)	8.6	(0.2)	10.1	(0.2)‡	77.4	(1.4)	86.3	(1.8)‡	10.2	(1.0)	61.0	(3.5)§
GVW¶	0.508	(0.45)	0.801	(0.49)	1.166	(0.77)	0.292	(0.27)*	0.801	(0.49)	1.166	(0.77)*	0.292	(0.27)	0.082	(0.27)*

*Significant at the 0.05 level.

†Breeding programs (BP) abbreviations are given in Table 1.

‡Least diverse programs for the traits measured at the plant level.

§Most diverse programs for the traits measured at the plant level.

¶GVW, variance in the genetic variance within breeding programs.

respectively. The latest maturing genotypes were from the winter program of Croatia and Denmark for two-row, and Canada Saskatchewan and the winter program of Croatia for six-row. Thus, in this study, the most extreme genotypes for any character were from breeding programs with extreme means for that character.

Several genotypes were among the top 10 for three or more traits evaluated in our conditions (see Table 3). Some of the two-row genotypes that performed the best were CA-SK-12 (HB329, spot blotch disease, test weight, and number of grains per spike), US-BSI-02 (Z010J016J, biomass at plant maturity, grain yield, and total number of spikes), and US-ND-02 (ND13299, spot blotch disease, biomass at plant maturity, and weight of 100 kernels). There were more single six-row genotypes with high performance, including lines from Canada Alberta (10: M79108001013, 12: M79108001013A, 15: H83030002, and 17: H87020011), with high values for biomass and grain yield, and low leaf rust incidence; Busch Ag Res (07: 6B98-9339, 09: 6B99-6639, and 15: 6B00-1499) with high values for grain yield and several other variables; North Dakota (07: ND231, 09: NDB125, and 14: Barless) with high performance lines for disease incidence and plant height; and Minnesota (11: Sep2-33 and 14: M99-68) with top lines for weight of 100 grains and several other traits.

Diversity within Breeding Programs

Days until anthesis, days until heading, test weight, weight of 100 grains, awn length, spike height, and number of grains were the only traits that showed a significant difference among breeding programs in the within-program genetic variance (Tables 1 and 2). The spring programs of Croatia and Germany, the two-row program of Busch Ag Res, the six-row winter program of Croatia, the six-row programs of Idaho and Minnesota were the least diverse breeding programs. Those programs were among the least

Table 3. Ten best genotypes for some variables of breeding interest: spot blotch disease (SB), leaf rust disease (LR), powdery mildew disease (PM), days until anthesis (DTA), plant height (HTOT), biomass (BWT), grain yield (YLD), number of spikes (NSPK), test weight (TWT), weight of 100 grains (W100G), and number of grains (NG). Breeding program abbreviations given in Table 1.

SB	LR	PM	DTA	DTA	HTOT	BWT	YLD	NSPK	TWT	W100G	NG
10 best (lowest value) genotypes two-row				10 best (highest value) genotypes two-row							
US-ID-05	US-ID-05	DE-05	CRO-WI-19	CRO-WI-11	CRO-WI-19	CRO-SP-20	CRO-SP-02	AU-AD-12	UY-12	AU-WE-11	CA-SK-12
CRO-WI-10	CRO-WI-10	DE-02	US-ND-20	DE-17	AU-AD-19	US-BS-18	US-WS-05	US-BS-18	AU-AD-08	UY-12	CA-AB-09
CA-SK-16	CA-SK-16	US-BSI-06	AU-WE-09	AU-WE-04	AU-WE-02	UY-04	UY-04	US-BSI-02	CA-SK-12	AU-WE-01	US-BS-11
US-ND-09	US-ND-09	US-BSI-15	AU-AD-12	DE-13	DE-17	US-ND-13	CRO-SP-18	SW-08	CA-AB-05	UY-02	CL-03
US-ND-02	US-ND-02	CRO-SP-03	AU-WE-16	CRO-WI-05	AU-AD-16	DE-12	CRO-SP-05	DE-09	US-BSI-13	US-ND-02	CA-AB-08
CA-SK-12	CA-SK-12	DE-03	AU-AD-09	DE-20	DE-06	CA-SK-05	UY-14	CRO-SP-07	UY-18	UY-18	CA-SK-03
US-BSI-17	US-BSI-17	DE-10	US-ND-19	CRO-WI-16	AU-AD-07	US-ND-02	UY-03	DE-14	UY-08	US-ND-17	SW-20
US-ND-03	US-ND-03	DE-07	AU-AD-05	CRO-WI-03	AU-AD-18	CA-SK-06	US-BSI-02	US-WS-20	CA-SK-19	US-ND-09	US-BSI-08
CA-AB-19	CA-AB-19	SW-11	AU-WE-07	AU-WE-05	US-WS-13	US-BSI-02	DE-12	SW-01	CL-07	AU-WE-16	CA-SK-10
UY-02	UY-02	CRO-WI-19	US-BSI-10	CRO-WI-07	US-BSI-14	CRO-SP-08	CRO-SP-08	US-WS-05	CA-SK-10	AU-AD-04	US-WS-10
10 best (lowest value) genotypes six-row				10 best (highest value) genotypes six-row							
US-ND-15	US-ND-15	CA-SK-13	US-ID-20	CA-SK-20	US-BS-02	US-BS-14	USA-MN-12	CA-AB-07	US-BS-15	USA-MN-06	US-BS-07
US-BS-13	US-BS-13	CA-AB-06	US-BS-08	US-BS-17	US-ND-14	CA-AB-10	CA-AB-12	US-ND-08	CA-AB-12	USA-MN-14	US-ND-10
CRO-WI-02	CRO-WI-02	CA-AB-14	USA-MN-09	CA-AB-03	US-BS-12	US-BS-15	US-BS-05	CA-AB-04	USA-MN-14	US-BS-11	US-ND-06
US-ND-14	US-ND-14	CRO-WI-01	USA-MN-19	CA-SK-21	CA-SK-14	CA-AB-17	USA-MN-07	CA-AB-17	US-BS-10	USA-MN-03	USA-MN-12
CA-AB-04	CA-AB-04	CA-AB-18	USA-MN-01	CA-SK-13	US-ND-08	US-ND-09	CA-AB-15	CRO-WI-13	USA-MN-17	USA-MN-13	USA-MN-11
US-BS-14	US-BS-14	US-ND-07	USA-MN-03	CA-AB-06	US-ND-15	CA-AB-15	US-BS-07	CA-AB-16	USA-MN-13	USA-MN-10	US-BS-14
US-ID-17	US-ID-17	US-ID-17	USA-MN-14	CRO-WI-14	US-ND-07	CA-AB-16	US-BS-15	CA-AB-01	USA-MN-19	USA-MN-05	CA-AB-20
US-ND-04	US-ND-04	US-ND-09	USA-MN-20	CRO-WI-01	US-ND-09	CA-AB-01	US-BS-09	CA-AB-10	US-BS-09	USA-MN-11	US-ND-07
US-ID-06	US-ID-06	CRO-WI-13	US-ND-06	CRO-WI-13	US-ND-13	CA-AB-12	CA-AB-10	CA-AB-15	CA-AB-13	US-BS-09	US-BS-11
CA-SK-15	CA-SK-15	USA-MN-05	USA-MN-18	CRO-WI-02	US-ND-11	US-BS-09	CA-AB-17	CA-AB-12	CA-AB-14	US-BS-13	US-ND-09

diverse for all the variables that had a significant difference in the within program genetic variance. Several programs were among the most diverse for three traits: Western Australia (DTA, DTH, and weight of 100 kernels), Canada Saskatchewan two-row (test weight, weight of 100 kernels, and spike height), and Sweden (test weight, awn length, and number of grains per spike). Denmark, Canada Saskatchewan six-row, and Canada Alberta six-row were the most diverse programs for two traits, and Washington and North Dakota six-row were the most diverse program for one trait.

The breeding programs included in this study are mainly breeding programs from developed countries with a strong focus on releasing cultivars. The presumably more diverse breeding programs that conduct breeding for less optimal conditions or low input situations such as ICARDA, Middle East, and Asia programs were not included. This limitation in the study could bias the results regarding the relative amount of diversity present in the breeding programs. It would be interesting to compare our results with studies from those breeding programs.

Although we did not look at the evolution of diversity in each breeding program, we found that some breeding programs had more diversity in traits than others. Studies that have evaluated the evolution of the genetic diversity in breeding programs have found either a decrease in the genetic diversity associated with breeding efforts (Ordon et al., 2005; Rasmusson and Phillips, 1997; Russell et al., 1997, 2000) or a nonsignificant decrease in genetic diversity (Khlestkina et al., 2006; Koebner et al., 2003; Malysheva-Otto et al., 2007; Ordon et al., 2005). We found that the Minnesota breeding program was one of the programs with lowest diversity for all traits in our study. This result was interesting when compared to the literature, where low diversity has been documented for Minnesota using pedigree information and observation of phenotypic traits (Rasmusson and Phillips, 1997). The breeding program of Germany was also one of the programs with the lowest diversity in our study. Germany is among European two-

row and six-row barleys identified to possess both a narrow gene pool (Russell et al., 1997) and no historical change in the genetic diversity (Malysheva-Otto et al., 2007) based on molecular markers. No previous information was found on the amount of diversity for the other programs with low diversity. Additionally, some of the most diverse breeding programs in our study, such as those from Sweden and Denmark, were examined in studies where no narrowing of the gene pool was detected (Malysheva-Otto et al., 2007). The purpose of our research was to study the differential amount of diversity for traits of breeding interest present in the breeding programs. It was out of the scope of our paper to study diversity at molecular markers. However, using the information from both morphological traits and neutral molecular markers would provide a better understanding of the loss of diversity in the breeding programs.

Several mechanisms could explain the difference in the levels of diversity for the traits examined here. For instance, maturity traits (DTA and DTH) showed higher diversity in Western Australia than in all of the other programs. One mechanism that could explain this is that Western Australia breeds for a wide set of environmental conditions, including differences in photoperiod. In other traits like awn length and spike height, the high diversity could be explained by the lack of direct selection on these traits. We would expect that traits under balancing selection would preserve more diversity than traits under strong directional selection because intermediate genotypes are preserved in the former case. Traits like test weight, weight of 100 grains, and number of grains could show high levels of diversity in programs that do not select directly for them, but only as a yield component. This could happen if for instance there is no premium for kernel plumpness or if the breeding program includes both feed and malt varieties.

Differences between Two-Row and Six-Row Types

The first two principal component axes explained 69% of the total variation. The first principal component axis and the cluster dendrogram largely separated two-row from six-row breeding programs (Fig. 1 and 2). All variables except grain yield and spike length had high loadings for the first

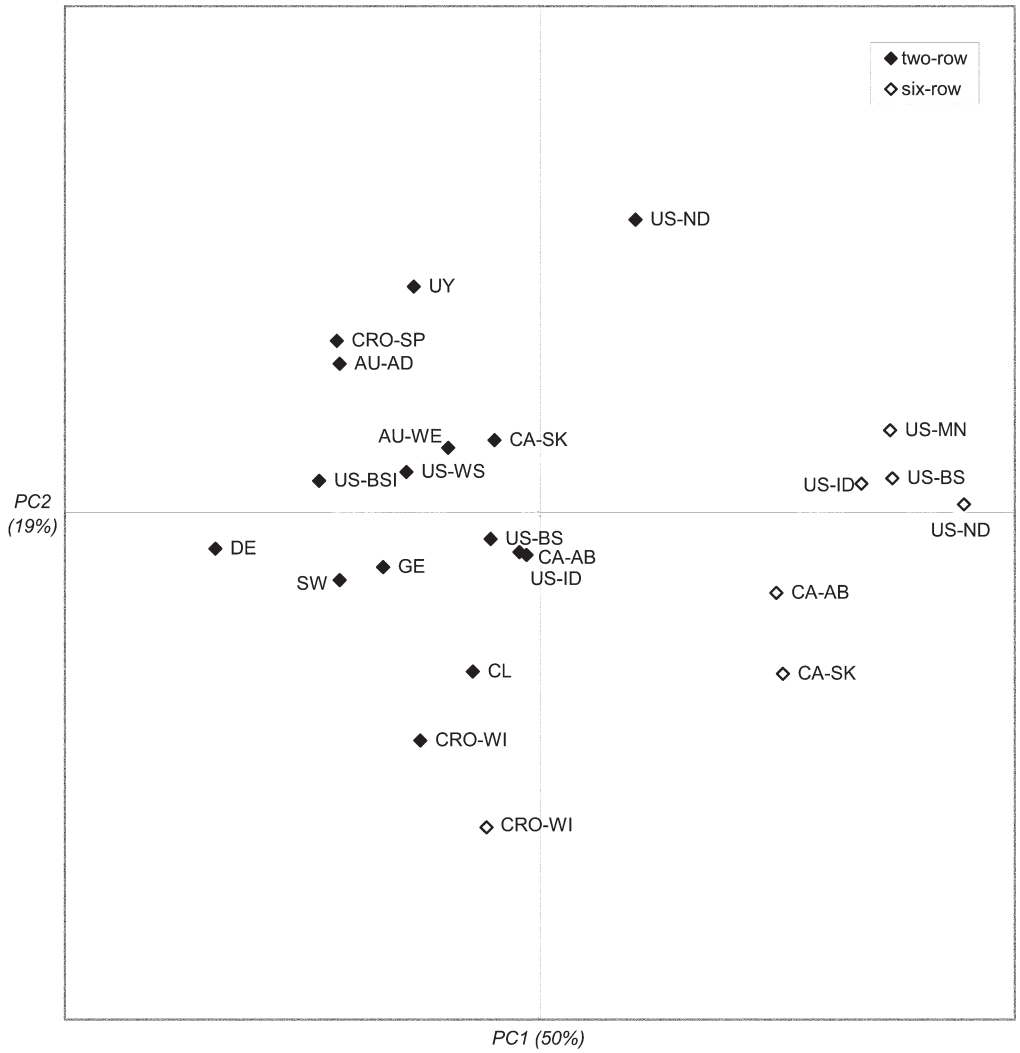

Figure 1. Representation of means of breeding programs in the first two principal component (PC) axes. Breeding program abbreviations are given in Table 1. Two- and six-row breeding programs are marked with filled and empty diamonds, respectively.

eigenvector (data not shown). The variables that most discriminated the two-row from six-row spring genotypes in the discriminant analysis were number of grains, spike length, flag leaf width, biomass, number of tillers, flag leaf length, spot blotch, and weight of 100 grains (Table 4).

The differentiation among two- and six-row types was expected because they form the two most distinct germplasm pools in barley (Powell et al., 1990; Takahashi et al., 1975). Even though there are only two epistatic loci involved in the distinction between two- and six-rows (Franckowiak and Lundqvist, 1997), due to historical patterns of breeding for usage—the gene pools were manipulated separately with little crossing—and geographical distribution—two-row is used for malting in most of the world, except in the United States and Mexico—there are differences at other quantitative traits between the groups (Takahashi et al., 1975). In our study, two-row genotypes had fewer grains per spike, but longer spikes, and higher weight of 100 grains. Additionally, they had more tillers and biomass, shorter and narrower leaves, and more spot blotch disease incidence. Other studies also found that two-row barley usually has more tillers and larger, heavier seeds, while six-row barley has more seeds per inflorescence (Marquez-Cedillo et al., 2001). Some studies explain this by pleiotropic effects (Allard, 1988), and others found linkage between those loci and quantitative traits such as yield, kernel plumpness, test weight, heading date, and plant height (Marquez-Cedillo et al., 2001). Because of the combination of previous information, historical germplasm usage and empirical results, we further analyzed data from the two head types separately. This was important to avoid differentiating the breeding programs by variables that separated two- vs. six-row types, and not necessarily by the variables that reflected the differences among breeding programs within two-row or six-row types. In the case of the cluster and principal component analysis, similar results were obtained when separate analyses were conducted for two- and six-row programs (data not shown).

Differences within Two-Row and Six-Row Types

The second axis of the principal component analysis discriminated breeding programs within head types. It explained differences between best and worst yielding programs in our environmental conditions, with high positive loadings on variables grain yield, test weight, and weight of 100 grains, and high negative values on maturity variables (DTA and DTH) for the second eigenvector (data not shown). In the discriminant analysis among two-row programs, the only variable that did not discriminate breeding programs was grain yield (Table 4). Spike characteristics (spike height, total number of spikes, spike

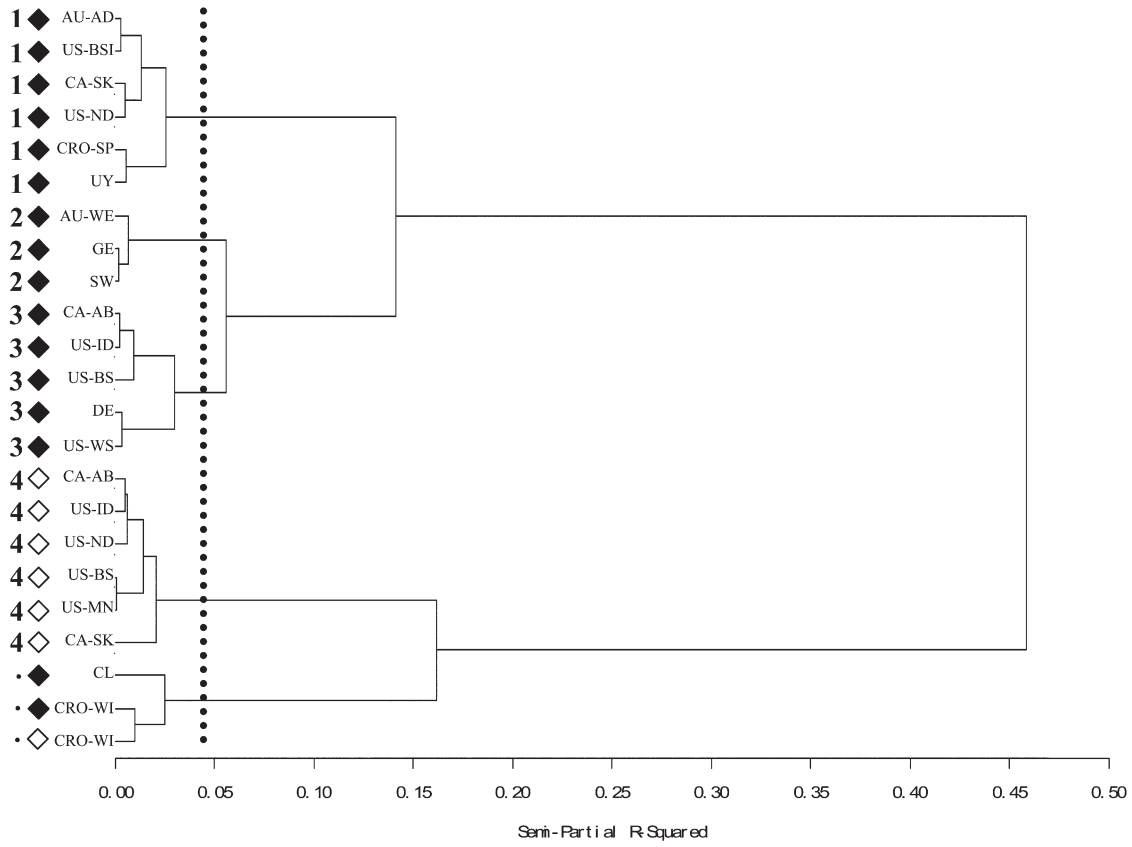

Figure 2. Cluster dendrogram of mean genotypic performance of breeding programs (abbreviations given in Table 1). The line indicates the separation of groups based on the clustering criterion and the number of each group is indicated on the left. Two- and six-row breeding programs are marked with filled and empty diamonds, respectively.

length, and number of grains per spike) as well as maturity, tillering, and yield components (test weight and number of grains per spike) were the variables that most discriminated among six-row breeding programs.

Table 4. Traits that most discriminate between two-row and six-row types, and between breeding programs within two-row and six-row types. Traits are number of tillers (NTIL), spot blotch disease (SB), leaf rust disease (LR), powdery mildew disease (PM), days until anthesis (DTA), days until heading (DTH), plant height (HTOT), biomass (BWT), grain yield (YLD), number of spikes (NSPK), test weight (TWT), weight of 100 grains (W100G), flag leaf length (FLL), flag leaf width (FLW), spike length (SLT), awn length (ALT), flag leaf height (FLH), spike height (SHT), peduncle length (PEDL), and number of grains per spike (NG).

Two-row vs. six-row			Breeding program (two-row)			Breeding program (six-row)		
Trait	*F*-value	*P*	Trait	*F*-value	*P*	Trait	*F*-value	*P*
NG	4823.3	<0.0001	PM	22.2	<0.0001	W100G	9.8	<0.0001
SLT	63.8	<0.0001	DTA	16.0	<0.0001	SHT	8.7	<0.0001
FLW	51.5	<0.0001	HTOT	13.3	<0.0001	NSPK	6.1	<0.0001
BWT	22.5	<0.0001	NTIL	6.1	<0.0001	SLT	4.7	0.0009
NTIL	5.7	0.0178	TWT	5.5	<0.0001	DTA	4.2	0.002
FLL	6.2	0.0134	W100G	4.5	<0.0001	NTIL	3.3	0.0109
SB	4.6	0.0329	BWT	3.8	<0.0001	W100G†	0.7	0.6346
W100G	2.5	0.1130	ALT	3.3	0.0002	FLW	2.3	0.0562
–	–	–	FLL	2.5	0.0051	TWT	1.9	0.1039
–	–	–	SB	2.2	0.0117	NG	1.9	0.1127
–	–	–	SHT	2.2	0.0129	–	–	–
–	–	–	FLH	2.7	0.0024	–	–	–
–	–	–	DTH	1.7	0.0606	–	–	–
–	–	–	FLW	1.7	0.0633	–	–	–
–	–	–	SLT	1.5	0.1112	–	–	–
–	–	–	NSPK	1.5	0.1356	–	–	–
–		–	NG	1.6	0.0931	–	–	–

†Trait removed during the STEPDISC procedure.

Grouping by Genotypic Performance

Cluster analysis indicated four groups of genotypic performance, formed mainly by head type (two-row or six-row), grain yield, and maturity traits (DTA and DTH), and did not reflect origin of the genotypes (Fig. 2). Group 1 included the high yielding with good kernel characteristics (high test weights and weight of 100 grains) and early maturing two-row programs (Adelaide, international program of Busch Ag Res, Canada Saskatchewan, North Dakota, Croatia spring, and Uruguay). Additionally, these programs had low incidence of leaf rust. Group 2 included the two-row programs with low biomass and grain yield, and short plants (Western Australia, Germany, and Sweden). Group 3 included all the remaining two-row programs (Canada Alberta, Idaho, Busch Ag Res, Denmark, and Washington), except Chile and Croatia winter. The breeding program of Chile had extreme mean values for most variables, did not group with other programs, and included only four genotypes. Therefore, it was considered an outlier and was not included in the discriminant analysis. Both winter breeding programs of Croatia also had extreme mean values for most variables, and since they were the only winter programs, and winter and spring types have been identified as some of the most distinct germplasm pools in barley (Matus and Hayes, 2002), with unique characteristics, we also excluded them from the discriminant analysis. Group 4 included all the six-row programs (Canada Alberta, Idaho, North Dakota, Busch Ag Res, Minnesota, and Canada Saskatchewan) except Croatia winter. Finally, the outliers, the Chile and winter programs of Croatia, grouped together. The groups within head type were maintained when separate analyses were performed by head type (data not shown). Therefore, the groups reflect true differences among breeding programs within two-row and six-row programs.

Grouping by Response to a Change in the Environment

Two- and six-row barleys tended to respond differently to the differences between environments (Fig. 3). Two-row programs had a more stable response to different environments; they had similar yields, grain characteristics, and maturity in both environments. The amount of difference in grain yield across locations shown in Fig. 3 was consistent with other variables, while breeding programs that were stable across environments for most variables were also stable for grain yield (data not shown). Six-row programs on the other hand had a more drastic response to the change in the environment, evident by larger bars in Fig. 3. These results are different from those obtained by García del Moral et al. (2003) and Le Gouis et al. (1999) who found that six-row cultivars were more stable across environments for yield components than two-row barleys. These difference could be explained by a combination of factors including the use of winter instead of spring types in these studies, the relative magnitude of the environmental differences (i.e., they used environments that ranged threefold in yield), the traits evaluated (i.e., yield component traits), and the specific genotypes and environments used. Regarding the specific traits, even though Le Gouis et al. (1999) reported six-row cultivars as more stable, they found that those cultivars have a more drastic response for the variable ears per square meter than two-row cultivars.

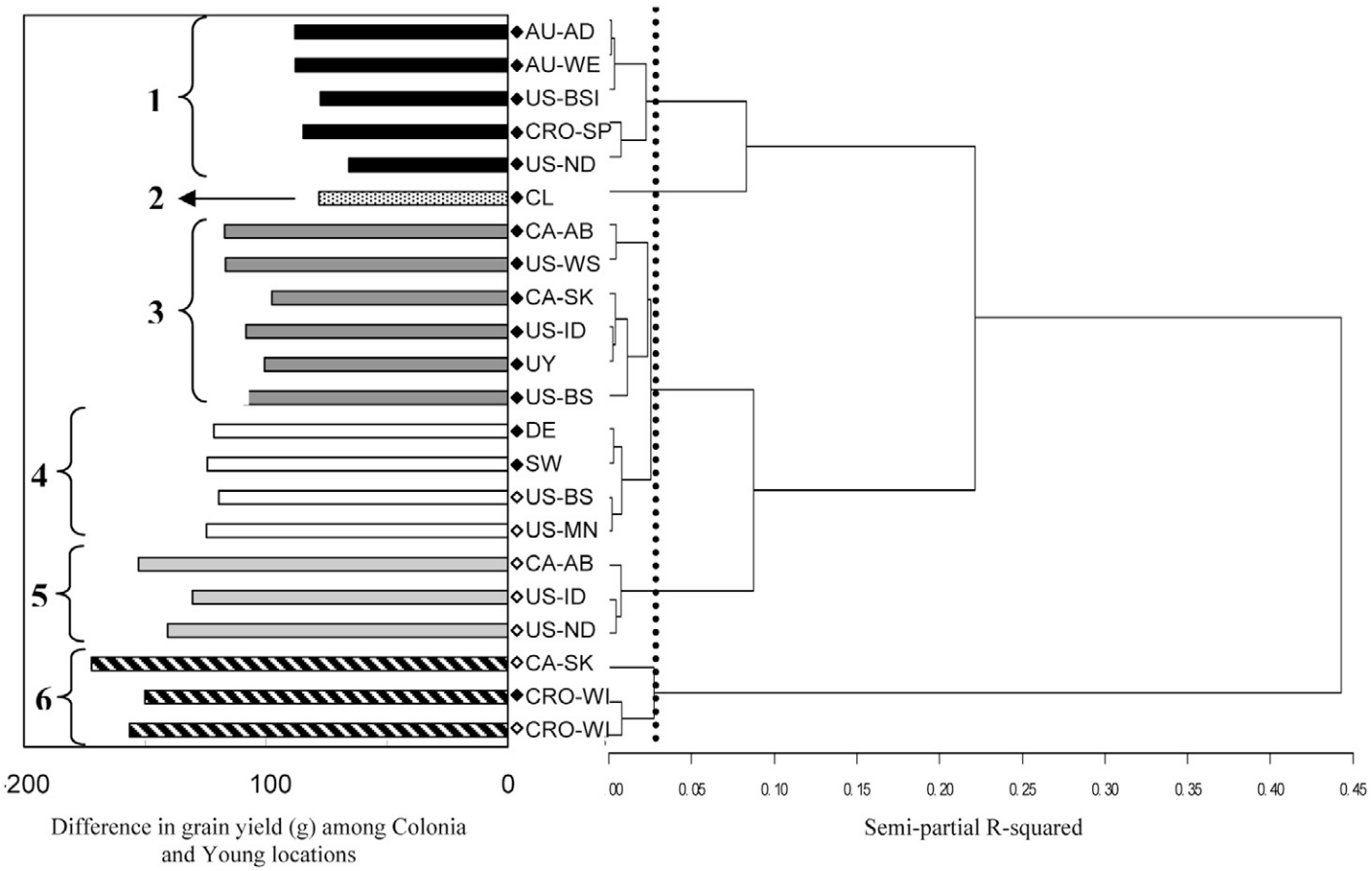

Figure 3. Cluster dendrogram of the difference of means across Colonia and Young locations for all variables showing the response to a change in the environment, and difference in grain yield among Colonia and Young locations. Breeding program abbreviations are given in Table 1. The line indicates the separation of groups based on the clustering criterion and the number of each group is indicated on the left. Two- and six-row breeding programs are marked with filled and empty squares, respectively.

Additionally, some studies reported more stable behavior of cultivars with high-quality malting traits than with medium-quality traits (Sparrow, 1971; Molina-Cano 1987; Molina-Cano et al., 1997) and two-row genotypes have better malting quality in general.

Six groups were produced by clustering breeding programs according to their differential response to the change in environments (Fig. 3). Group 1 was formed by two-row programs including AU-AD, AU-WE, US-BSI, CRO-SP, and US-ND. Group 2 included only CL, which behaved very differently from other programs. Group 3 was formed by two-row programs, including CA-AB, US-WS, CA-SK, US-ID, UY, and US-BS. Group 4 included both two- and six-row programs: DE and SW for two-row, and US-BS and US-MN for six-row. Group 5 included only six-row programs, CA-AB, US-ID, and US-ND. Finally, Group 6 included CA-SK and the two- and six-row programs of CRO-WI.

While grouping by performance was not related to the geographical location of the breeding programs (i.e., the two Australian programs were assigned to different groups as were the two Canadian breeding programs, and European and other American breeding programs were also found in several groups), grouping by response to a change in the environment was related to the geographical location of the breeding programs (i.e., both Australian breeding programs were assigned to the same group, and both Canadian programs and European programs were also assigned to the same groups). The combination of grouping by performance and by response to the change in the environment is relevant in the definition of MTS, and discussed below.

Genotype × environment interactions are widespread in nature (Allard and Bradshaw, 1964) and significant genotype × environment and breeding program × environment interactions were found in this study (data not shown). However, those interactions were mainly magnitude differences across environments, and not crossover interactions. Furthermore, principal component and cluster analysis by environment produced the same groups (data not shown). Principal component and cluster analysis using variables in different environments as different traits did not change the grouping of the breeding programs. Therefore, we believe that genotype by location or breeding program by location interactions did not influence the results we report.

Mega-Targets of Selection

To identify data-driven groupings of breeding programs that would benefit from germplasm exchange enhancing

the genetic progress, we conducted two distinct analyses. First, we grouped breeding programs by their performance in the environments studied. Four groups (and some outliers) were produced by genotypic performance: three groups of two-row barley differentiated by grain yield and maturity, and one group of six-row barleys. Clusters based on genotypic performance do not necessarily group breeding programs that would benefit from germplasm exchange because genotypes from two breeding programs could both perform poorly in an environment due to different causes. For example, one set of genotypes might be limited because of traits that promote general adaptation, like diseases, the other by photoperiod conditions such that the programs are not adapted to the same environmental conditions. Therefore, in a second approach, we grouped breeding programs by their response to a change in the environment. Again, four groups (and some outliers) were produced by their response to the change in the environment: two groups of two-row barley, one group of two- and six-row barley, and one group of six-row barley. These groups were related to the geographical location of the breeding program.

Using both criteria, we identified three MTS. These are sets of breeding programs that belong to the same groups of genotypic performance and response to selection (Fig. 2 and 3). The first MTS includes high-yielding two-row programs with good kernel properties (i.e., Group 1 of genotypic performance) that have a small response to the change in the environment (i.e., Group 1 of response to the change in the environment). The breeding programs included in this group are Adelaide, the international program of Busch Ag Res, North Dakota, and the spring program of Croatia. The second MTS includes the two-row programs that have an average performance for all variables (i.e., Group 3 of genotypic performance) and that have the largest response to a change in the environment (i.e., Group 3 of response to a change in the environment). The breeding programs included in this group are Canada Alberta, Idaho, Washington, and Busch Ag Res program. Finally, the third MTS comprises the six-row breeding programs that have a drastic response to the change in the environment. The programs included in this group are Canada Alberta, Idaho, and North Dakota. Obtaining only one MTS for six-row barley provides only little information for germplasm exchange decisions for six-row breeding programs. Only those programs included in the MTS group have clear indications for exchange; the other programs do not have a clear direction as to with whom exchange would be beneficial. Exchanging germplasm within MTS should be beneficial because we expect genotypes to be adapted to similar conditions and to perform similarly. Additional pairs of programs that could benefit from germplasm exchange are two-row Canada Saskatchewan and Uruguay, and six-row Busch Ag Res and Minnesota.

Mega-targets of selection are analogous to mega-environments (ME). The ME group of environments that produce the same rank of the genotypes (Yan et al., 2000). Genotypic evaluation in any of the environments within an ME is equivalent because there is no crossover interaction for environments within an ME (DeLacy et al., 1994; Trethowan et al., 2001). In MTS, groups of breeding programs are formed such that exchanging germplasm material within a group will produce genotypes that are well adapted and respond similarly to the new environmental conditions. Similarly to ME, where using more genotypes and environments allows for broader generalization, in MTS, using more contrasting environments and breeding programs would allow for broader generalization. Our study was limited by the number of environments used for evaluation and by how similar those two environments were. Therefore, general recommendations for germplasm exchange cannot be made from this study. However, the main objective of our work was to present the methodology for grouping breeding programs and having more environments would not allow us to fulfill this objective any better. Additionally, we were trying to group breeding programs and not environments, and we evaluated 23 breeding programs, a considerable number. Finally, there are numerous reports in which only a small number of genotypes and/or environments were used to study ME (Blanche and Myers, 2006; Robins et al., 2007; Samonte et al., 2005). Those studies are valuable within the genetic background of the genotypes and the environments evaluated. We used two environments with distinct soil types, mean temperature, precipitation, and disease pressure.

CONCLUSION

Exchange of genetic material is essential for enhancing genetic gain in a breeding program. We evaluated two relevant aspects of breeding programs that will aid in germplasm exchange. First, we evaluated the amount of genetic diversity within breeding programs. We found significant genotypic variation within breeding programs for all 20 morphological traits we measured. There were differences in the amount of genotypic variation within breeding programs for seven of these traits. We were able to identify breeding programs that had systematically more or systematically less diversity. Note that this diversity criterion does not provide an indicator to establish whether breeding programs are more or less successful. Success criteria would depend on each program's objectives and would therefore vary from program to program. Second, we established, in a data-driven way, groups of breeding programs that would benefit from germplasm exchange (i.e., MTS). The methodology we propose groups breeding programs by their performance and their response to changes in the environment providing groups of breeding programs with similar performance and similar

adaptations. Therefore, we would expect that exchange of germplasm within MTS would produce adapted genotypes with high yields.

Ideally for germplasm exchange, we would require elite, well-adapted germplasm with different alleles at loci of interest. We evaluated elite germplasm and provided a methodology to identify sets of breeding programs that are adapted to similar conditions, and therefore with whom germplasm exchange could be favorable. We also evaluated the performance of the genotypes to identify high yielding materials and we evaluated the amount of genetic diversity present in each program. Although outside the scope of this study, it would be useful to also identify genotypes with different alleles at loci of interest.

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